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Classification of the Bivalvia

By Norman D. Newell[1]

INTRODUCTION

The Bivalvia are wholly aquatic benthos that have undergone secondary degeneration from the condition of the ancestral mollusk (possibly, but not certainly, a monoplacophoran-like animal; Yonge, 1953, 1960; Vokes, 1954; Horný, 1960) through the loss of the head and the adoption of a passive mode of life in which feeding is accomplished by the filtering of water or sifting of sediment for particulate organic matter. These adaptations have limited the evolutionary potential severely, and most structural changes have followed variations on rather simple themes. The most evident adaptations are involved in the articulation of the valves, defense, anchorage, burrowing, and efficiency in feeding. Habitat preferences are correlated with the availability of food and with chemistry, temperature, agitation and depth of water, and with firmness of the bottom on, or within, which they live. The morphological clues to genetic affinity are few. Consequently, parallel trends are rife, and it is difficult to arrange the class taxonomically in a consistent and logical way that takes known history into account.

The problem of classifying the bivalves is further complicated by the fact that critical characters sought in fossil representatives commonly are concealed by rock matrix or are obliterated by the crystallization or dissolution of the unstable skeletal aragonite. The problem of studying mor-

[1] Curator, Department of Fossil Invertebrates, the American Museum of Natural History; Professor of Geology, Columbia University in the City of New York.

phological details is especially difficult among the older fossils which should provide evidence of relative times of phyletic divergence. Among these, morphological details generally are inadequately known, partly as a result of limitations of the materials but even more as the result of insufficient work on the group and lack of application of adequate skills and preparation techniques. In all the history of work on the older bivalves, there have been few examples of outstanding morphological work on these fossils. Sound morphological studies are essential for classification and phylogeny.

The present outline classification is an attempt to synthesize and integrate the best features of the most widely used systems. It is not basically new nor is it based on adequate phylogenetic information.

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FAMILY-GROUP CATEGORIES

Many of the major fossil and living groups, now generally regarded as superfamilies, are highly distinctive and were discriminated by the middle of the nineteenth century. Several were known even by vernacular names long before the time of Linnaeus. It is evident that many of the family-group taxa have been astonishingly conservative, with long and continuous records that extend far back into the Paleozoic where well-preserved specimens may be relatively scarce and origins of higher categories are generally conjectural. Where the fossil record is good, there is abundant evidence that general shell characters in many groups have been quite stable, through hundreds of millions of years, which is contrary to a view sometimes voiced that the soft anatomy is somehow more revealing of affinities than shell morphology and that shell characters alone are inadequate and unreliable as indicators of phylogeny.

THE HIGHER CATEGORIES

The building blocks of bivalve taxonomy have been the family groups which, in general, have not been very controversial. Real difficulties arise, however, when attempts are made to bring together well-defined families into orders and subclasses. Excellent reviews of the history of efforts to devise a stable system of bivalve higher categories have been published by Haas (1929–1956), Iredale (1939), Purchon (1958), Cox (1960), and Morton (1963), and are not taken up in detail here. It is sufficient to say that, lacking graded morphological series of living or fossil forms joining many of the family-group taxa, systematists have sought more or less arbitrarily to base ordinal groupings on single-organ systems. But most of such traits are now known to be individually plastic and are demonstrably variable within families or even within genera. The experience of more than two centuries of work on the subject encourages the view that a simple key-like classification of the bivalves cannot adequately reflect their relationships at the level of orders and subclasses.

THE EARLY SEARCH FOR TAXOBASES

The degree of fusion of the mantle margins, together with the character and number of the resulting apertures or siphons, was regarded by Linnaeus (1758) as a primary basis for the discrimination of orders. In this belief, he was followed for a time by many students: for example, Cuvier (1797, 1800), Lamarck (1801), Duméril (1806), Fleming (1822, 1828), Latreille (1825), d'Orbigny (1843–1847), Woodward (1851–1856), Adams and Adams (1854–1858), and Zittel (1881–1885).

In addition to the lack or possession of well-developed siphons, Lamarck (1812) also stressed the progressive reduction and loss of the anterior adductor in some groups as important and useful, as did Philippi (1853) and Zittel (1881–1885). Gray (1821) and Lankester (1883) thought that the form and function of the foot were a reliable basis for the recognition of suprafamilial groups. Linnaeus (1758) and d'Orbigny (1843–1847) also used the equality or inequality of the valves as a convenient taxonomic criterion.

The objective of these efforts, of course, was utilitarian, with little thought of phyletic history. The characters enumerated still figure prominently in all classifications but are now generally regarded as supplementary features that may appear independently in unrelated groups. Loss of the anterior muscle (as in the Pectinidae and the Tridacnidae), or cementation by one valve and acquisition of an oyster-like growth

form (*Ostrea*, *Hinnites*, *Mulleria*), are illustrations of parallel adaptations in groups that are otherwise unlike.

CONTRIBUTIONS FROM PALEONTOLOGISTS

Stoliczka (1870–1871), a paleontologist who was impressed by the general stability and homogeneity of form and structure of family groupings of bivalves throughout their history, proposed to base higher categories on an over-all resemblance to a type genus, and he established nine orders, the names of which were based on the stems of generic names. This taxonomic device had already been experimented with by Rafinesque (1815), Férrusac (1822), and Adams and Adams (1854–1858). Experience showed that it had a sound basis, and the orders of Stoliczka, with modifications and additions, have become the superfamilies of later workers.

Over the years, the list of generally recognized major groups has grown from the nine orders in Stoliczka's classification to the 47 superfamilies in the present treatment, with others sure to follow as the study of Paleozoic bivalves progresses. Throughout the nineteenth century the unwieldy number of family taxa prompted many efforts to regroup the class into a few convenient morphological divisions.

The paleontologists Neumayr (1884, 1891), Steinmann (1888), Dall (1889, 1895, 1896–1900, 1913), and Douvillé (1896, 1907, 1912, 1913) introduced the historical-phylogenetic point of view into efforts to classify the bivalves. They demonstrated that general shell form and details of the articulating apparatus, that is, the hinge teeth plus the ligament, were frequently quite stable through time, but they also pointed out many exceptions, as, for example, the highly variable hinges of the dysodonts and the fresh-water mussels (Unionacea). The French paleontologist Bernard (1895, 1896a, 1896b, 1897, 1898) shared these views and undertook elaborate studies of the ontogenies of the hinge in several living bivalves. Unfortunately, his work was interrupted by his early death, and this promising field of investigation has since been neglected.

Dall and Douvillé both advocated close attention to the total organism, and they believed that the findings concerning the comparative anatomy of living species could be harmonized with paleontological evidence based on geological chronology and shell characters. To them it was obvious that special attention must be given characters that are preserved in the fossil record if the historical facts of bivalve evolution are to be given due recognition in classification. These authors also made some limited use of the poorly understood differences in shell fabric, or microstructure, later described in some detail by Bøggild (1930) and Oberling (1955, 1964).

It seems clear that shell fabric is important contributory evidence (e.g., all unionaceans have prismato-nacreous shells; all oysters possess foliaceous calcite shells), but the full phylogenetic implications have yet to be worked out. Unfortunately, original shell microstructures are rarely preserved in bivalves older than the Pennsylvanian, and they frequently are destroyed even in geologically quite young fossils.

Douvillé's great contribution was to emphasize broad adaptive levels in reaching phylogenetic conclusions about the bivalves. In this he recognized the hazard of confusing examples of similar adaptation with close genetic affinity, and he tried to make use of all lines of evidence. He did not complete a formal taxonomic arrangement of the bivalves, but his work was incorporated in a classification of the Tertiary bivalves by A. Morley Davies (1935) that stands as a monument to Douvillé. Unfortunately, Davies' work did not consider, nor will it accommodate, many of the pre-Tertiary forms.

Douvillé distributed all bivalves among three branches according to three main modes of life. These were:

1. The "normal" or vagrant epifaunal bivalves.
2. Fixed, or "sedentary" epifaunal forms, either suspended by a byssus or cemented by one valve for part of the life span.
3. The burrowing, or boring, infaunal bivalves (desmodonts of Neumayr).

Douvillé recognized that many members of these three branches had undergone secondary radiation that resulted in structural similarities among unrelated stocks, the details of which he tried to understand by combining studies of comparative anatomy and paleontology (Davies, 1933). Paleontologic and morphologic evidence supports the probable unity of most of his "sedentary" branch, but his "normal" and "burrowing" branches are not very homogeneous historically or even anatomically (fig. 1).

THE PELSENEER SCHOOL

In spite of the considerable amount of paleontologic evidence that was early available and general agreement that a phylogenetic approach to classification must take into account all lines of evidence, there developed a school of anatomists that ignored the fossil evidence and the integrity of superfamilies as defined by aggregate characters and turned to comparative studies of the bivalve ctenidia (fig. 2) as a primary basis for higher classification (Fischer, 1880–1887; Pelseneer, 1889, 1891, 1906, 1911; Ridewood, 1903).

More recently, Adkins (1936–1938) has classified the bivalves according

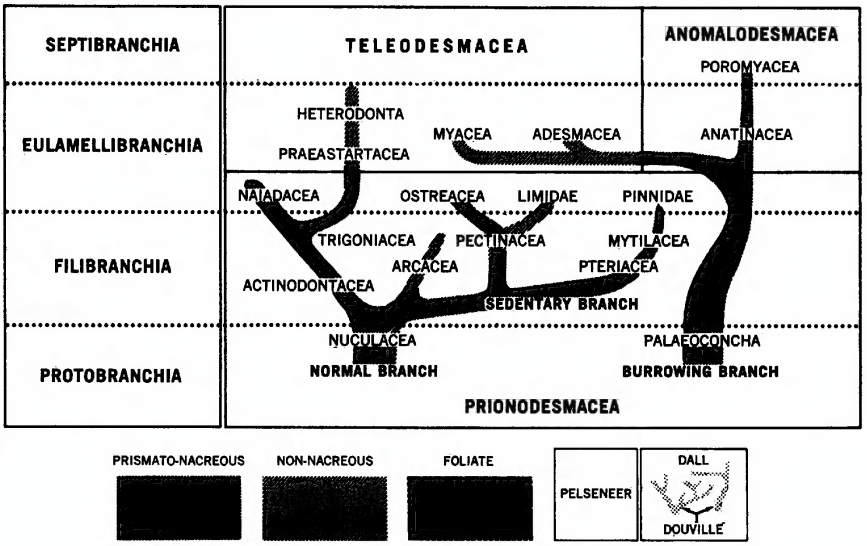

FIG. 1. Comparison of classifications of Dall and Douvillé (based in part on geologic history), with the "horizontal" classification of Pelseneer based mainly on ctenidial grade.

to whether they possess one or another of two types of laterofrontal cilia on ctenidial filaments. Purchon (1958) has based a system on stomach type in which he recognizes five grades. Stasek (1963) preferred, as a primary taxobasis, the degree of association of ctenidia and labial palps (table 1). The philosophic objection to these modes of approach is that they do not take into account the total organism, and they provide no grounds for the recognition of examples of parallel evolution. The practical objection is that they cannot be applied to fossils, and they make no provision for the evaluation of paleontologic evidence which is the court of final appeal with respect to the phylogeny of the bivalves.

Studies of comparative anatomy are of biologic interest and of course are essential for arriving at phylogenetic conclusions. They are, however, only supplementary and cannot alone provide the needed evidence of the historical course of evolution. Ridewood (1903) showed that there is a sequence of stages in the union of adjacent gill filaments and that identical grades of gill structure have been acquired in bivalves that otherwise are unlike. Furthermore, other bivalves closely alike in many characters may have different grades of ctenidia. For example, the Ostreacea, Pinnacea, and Limacea have gills of the eulamellibranch grade, although they have much in common with the Pectinacea, Mytilacea, and Anomiacea which

DALL, 1913	THIELE, 1934-1936		FRANC, 1960		COX, 1960		NEWELL, NEW, HEREIN	
PRIONODESMACEA	TAXODONTA		PROTOBRANCHIA	NUCULIDAE NUCULANIDAE MALLETIIDAE	PROTOBRANCHIA	PALAEOTAXODONTIDA	PALAEOTAXODONTA	NUCULOIDA
				SOLEMYIDAE		LIPODONTIDA	CRYPTODONTA	SOLEMYOIDA
						CRYPTODONTIDA		PRAECARDIOIDA
	ANISOMYARIA		FILIBRANCHIA	TAXODONTA	PTERIOMORPHIA	EUTAXODONTIDA	PTERIOMORPHIA	ARCOIDA
				ANISOMYARIA		ISOFILIBRANCHIDA		MYTILOIDA
						PTEROCONCHIDA		PTERIOIDA
						COLLOCONCHIDA		
	EULAMELLIBRANCHIA	SCHIZODONTA	EULAMELLIBRANCHIA	SCHIZODONTA	HETEROCONCHIA	SCHIZODONTIDA	PALAEOHETERODONTA	TRIGONIOIDA
						NAIADIDA		UNIONOIDA
TELEODESMACEA		EXTINCT		EXTINCT		PANTODONTIDA		ACTINODONTOIDA
		EXTINCT		RUDISTES		PACHYODONTIDA	HETERODONTA	HIPPURITOIDA
		HETERODONTA		HETERODONTA		HETERODONTIDA		VENEROIDA
		ADAPEDONTA		ADAPEDONTA		ASTHENODONTIDA		MYOIDA
ANOMALODESMACEA		ANOMALODESMATA		ANOMALODESMACEA		EUDESMODONTIDA	ANOMALODESMATA	PHOLADOMYOIDA
				SEPTIBRANCHIA		SEPTIBRANCHIDA		POROMYOIDA

FIG. 2. Classification of the bivalves designed for the "Treatise on invertebrate paleontology" compared with some recent classifications.

have filibranch gills. In four families, the Arcidae, Anomiidae, Pteriidae (Aviculidae), and Spondylidae, Ridewood found that one or two species had advanced a step beyond the rest of the family. The family-group taxa, based on multiple character complexes, are thereby fragmented. These facts are adequate evidence of parallel evolution through a series of functional grades and are not indicative of relationship. Pelseneer (1906), in his taxonomic treatment, divided the anisomyarians (considered together with the Arcoida by many paleontologists as a phylogenetic unit, the Pteriomorphia) according to grades of gill structure into the Filibranchia and Eulamellibranchia. Later (Pelseneer, 1911) recognizing the incongruity of the resulting associations, he redistributed some of the families in an intermediate group, the Pseudolamellibranchia, which was heterogeneous as regards grade of gill structure, combining families with eulamellibranchiate gills (Ostreidae, Limidae, Pinnidae) and others possessing filibranch gills (Vulsellidae, Pteriidae, and Pectinidae). Thus, he abandoned gill structure as the primary anatomical basis in favor of over-all resemblance. A comparison of Pelseneer's scheme with the classifications of Dall and Douvillé is shown in figure 1. A modified version of Pelseneer's 1906 treatment of the bivalves is still followed in a leading zoological treatise (Franc, 1960), in which the Filibranchia still contain some forms with eulamellibranch gills (Pinnidae, Limidae, Ostreidae)

TABLE 1

SOME CHARACTERISTICS OF EXTANT BIVALVE SUPERFAMILIES

Subclasses and Superfamilies	Gill Grade				Gill Cilia		Stomach Type					Labial Palps			Shell Microstructure			
	Protobranch	Filibranch	Eulamellibranch	Septibranch	Atkins, Type 1	Atkins, Type 2	Purchon, Type 1	Purchon, Type 2	Purchon, Type 3	Purchon, Type 4	Purchon, Type 5	Stasek, Type 1	Stasek, Type 2	Stasek, Type 3	Nacreous	Cross Lamellar	Foliate	Homogeneous
Palaeotaxodonta																		
Nuculacea	x	—	—	—	x	—	x	—	—	—	—	x	—	—	x	x	—	—
Nuculanacea	x	—	—	—	—	—	x	—	—	—	—	—	—	—	—	—	—	x
Cryptodonta																		
Solemyacea	x	—	—	—	—	—	?	—	—	—	—	—	—	—	—	—	—	x
Pteriomorphia																		
Arcacea	—	x	—	—	—	x	—	—	x	—	—	—	—	x	—	x	—	—
Limopsacea	—	x	—	—	—	x	—	—	x	—	—	—	—	—	—	x	—	—
Mytilacea	—	x	—	—	x	—	—	—	x	—	—	x	—	—	x	—	—	—
Pteriacea	—	x	—	—	—	x	—	—	x	—	—	—	—	x	x	x	—	—
Pinnacea	—	—	x	—	—	x	—	—	x	—	—	—	—	—	x	—	—	—
Pectinacea	—	x	—	—	—	x	—	—	—	x	—	—	—	x	x	x	x	—
Anomiacea	—	x	—	—	—	x	—	—	—	x	—	—	—	x	—	—	x	—
Ostreacea	—	—	x	—	—	x	—	—	x	—	—	—	—	x	—	—	x	—
Limacea	—	—	x	—	—	x	—	—	—	x	—	—	—	—	—	x	—	—
Palaeoheterodonta																		
Unionacea	—	x	—	—	x	—	—	—	—	x	—	x	—	—	x	—	—	—
Trigoniacea	—	x	—	—	x	—	—	—	—	x	—	x	—	—	x	—	—	—
Heterodonta																		
Lucinacea	—	—	x	—	x	—	—	—	—	x	—	—	—	x	—	x	—	—
Leptonacea	—	—	x	—	x	—	—	—	—	—	—	—	—	x	—	x	—	—

TABLE 1 (*Continued*)

Subclasses and Superfamilies	Gill Grade				Gill Cilia		Stomach Type					Labial Palps			Shell Microstructure			
	Protobranch	Filibranch	Eulamellibranch	Septibranch	Atkins, Type 1	Atkins, Type 2	Purchon, Type 1	Purchon, Type 2	Purchon, Type 3	Purchon, Type 4	Purchon, Type 5	Stasek, Type 1	Stasek, Type 2	Stasek, Type 3	Nacreous	Cross Lamellar	Foliate	Homogeneous
Cyamiacea	—	—	x	—	x	—	—	—	—	x	—	—	—	x	—	x	—	—
Tellinacea	—	—	x	—	x	—	—	—	—	—	x	—	—	x	—	x	—	—
Solenacea	—	—	x	—	x	—	—	—	—	—	x	—	—	x	—	x	—	—
Mactracea	—	—	x	—	x	—	—	—	—	—	x	—	—	x	—	x	—	—
Cardiacea	—	—	x	—	x	—	—	—	—	—	x	—	x	—	—	x	—	—
Tridacnacea	—	—	x	—	x	—	—	—	—	—	x	—	—	—	—	x	—	—
Carditacea	—	—	x	—	x	—	—	—	—	x	—	—	x	—	—	x	—	—
Crassatellacea	—	—	x	—	x	—	—	—	—	x	—	x	—	x	—	x	—	—
Arcticacea	—	—	x	—	x	—	—	—	—	—	—	—	—	—	—	x	—	—
Dreissenacea	—	—	x	—	x	—	—	—	—	—	—	—	—	—	—	x	—	—
Glossacea	—	—	x	—	x	—	—	—	—	—	x	—	x	—	—	x	—	—
Corbiculacea	—	—	x	—	x	—	—	—	—	—	x	—	—	—	—	x	—	—
Veneracea	—	—	x	—	x	—	—	—	—	—	x	—	x	x	—	x	—	—
Chamacea	—	—	x	—	x	—	—	—	—	x	—	—	x	—	—	x	—	—
Myacea	—	—	x	—	x	—	—	—	—	—	x	—	—	x	—	x	—	—
Pholadacea	—	—	x	—	x	—	—	—	—	—	x	—	—	x	—	x	—	—
Anomalodesmata																		
Pholadomyacea	—	—	x	—	x	—	—	—	—	—	—	—	—	—	x	—	—	—
Pandoracea	—	—	x	—	x	—	—	—	—	x	—	—	—	x	x	—	—	—
Clavagellacea	—	—	x	—	x	—	—	—	—	x	—	—	—	x	x	—	—	—
Poromyacea	—	—	—	x	—	—	—	x	—	—	—	—	—	x	x	—	—	—

and the Eulamellibranchia include others with filibranch gills (Trigoniidae). These groups simply illustrate mosaic evolution in which gill characters have evolved at differing rates in different lines. The original purpose of Pelseneer, to provide a simple method of keying the various bivalves according to grade of gill structure, is thus defeated, and there is no semblance of consistency in his search for a natural classification.

HORIZONTAL VERSUS VERTICAL SYSTEMS

In spite of general doubts about the validity of Pelseneer's orders of Bivalvia, Yonge (1959), Cox (1959), Owen (1959), and Purchon (1959), in a symposium on primitive bivalves, recently marshalled evidence of the homogeneity of the bivalves with primitive comblike gills, the Protobranchia, which they would elevate from ordinal status to a subclass of the Bivalvia. All the other bivalves they would segregate in one or more additional subclasses. The Protobranchia are based on ctenidial characters shared by the single extant family, the Solemyidae, and the nuculoids. Otherwise dissimilar, the two groups are characterized by simple gills, which in the nuculoids do not function in feeding. Structurally, they are reminiscent of the gills of certain gastropods. In *Solemya*, however, the gills also are used in feeding.

Both *Solemya* and the nuculoids are detritus feeders, unlike the majority of bivalves which strain suspended material from water. Thus, the protobranchs share in common the quality of primitiveness of the ctenidia. Here the similarity ends. The nuculoids, clearly a homogeneous group, differ in almost every other feature from *Solemya*. Both groups are extremely ancient, having been separate for at least a half a billion years, and there is no paleontologic evidence that either was derived from the other. Were they closely related, the fossil record should show some evidense of parallel shell trends, but the shells have always been quite unlike and remarkably stable.

The Solemyidae and the nuculoids apparently have shared the same habitat and have occupied similar niches throughout their known history without any tendency to develop similar shell characters. Since they are morphologically unlike, are not connected by intermediate forms, and have reacted differently within the same habitat, one might infer that they are in fact only distantly related to each other. Classifying these two groups together simply because of similarities in one organ (gill structure) is not more defensible than classing all nacreous shells or all monomyarian shells together. Modern work on the genus *Solemya* tends to emphasize the innumerable points of difference from the nuculoids. Horizontal classi-

fication based on a single-organ system of course has an element of utility, but it does not reflect the intricacies of phylogeny.

In the light of existing knowledge about the bivalves, an over-all phylogenetic classification has not been devised, and experience shows that a simple classification free from innumerable inherent inconsistencies cannot be achieved as yet. Ultimately, the older fossils will provide the needed evidence for grouping morphologically dissimilar superfamilies on the basis of common origin. This may be accomplished only by working upward through genus, family, superfamily, order, and subclass, with a critical eye to the fossil evidence. A wholly satisfactory classification cannot be obtained by arbitrarily forcing family-group taxa into ready-made higher categories.

With some noteworthy modifications, the groupings adopted herein are parallel to those prepared by L. R. Cox (1960), most of which, in turn, were based on work that had gone before.

NAME OF THE CLASS

Even the name to be applied to the bivalve mollusks has been a source of widespread disagreement. The malacologists of the world have in recent years been about evenly divided in preferences between the two terms Pelecypoda Goldfuss, 1820, and Lamellibranchiata (or Lamellibranchia) de Blainville, 1824 (Lamellibranches, 1814), and there seems to be no possibility of winning universal adoption of either of these two names. Following the example of Haas (1929-1956) and Thiele (1934-1935) there is now a strong swing toward compromise on Linnaeus' term Bivalvia Linnaeus, 1758 (Yonge, 1959; Purchon, 1959; Franc, 1960; Ebersin, 1960; Cox, 1960; Morton, 1963; Stasek, 1963). This name is not only the oldest formally applied to the class, but it has the merit of possessing a familiar English cognate, "bivalve," which is meaningful to the layman. Generally, there is little confusion with other bivalve groups such as brachiopods and ostracodes (or even some gastropods) which are not customarily termed bivalves without a qualifying adjective. In any case, the name of the class is not intended to be an anatomical description. If desirable, the vernacular terms "pelecypod," or "lamellibranch" may continue to be employed by those who prefer them to "bivalve."

THE SUBCLASSES

The function of subclasses is to provide a few major divisions for convenience in discussion and taxonomic sorting and ultimately to distinguish

the trunk lines of phylogenetic descent. The last-named objective cannot be fully attained at the present time with the bivalves. The treatment followed here (fig. 2) employs six major divisions, at least two of which (Palaeotaxodonta, Pteriomorphia) are considered more or less natural groupings by many paleontologists and neontologists. The other four are somewhat artificial.

SUBCLASSES
Palaeotaxodonta Korobkov, 1954
Cryptodonta Neumayr, 1884
Pteriomorphia Beurlen, 1944
Palaeoheterodonta Newell, new herein
Heterodonta Neumayr, 1884
Anomalodesmata Dall, 1889

The Palaeotaxodonta comprise the nuculoids, a compact group characterized by a primitive taxodont hinge and protobranch ctenidia which function almost solely in respiration. All are soft-bottom detritus feeders, with representatives of both epifauna and infauna, each with appropriate adaptations. The nuculoids have long been considered to be the most primitive living bivalves, but they are not known to be the most ancient. There is no direct evidence that they gave rise to other radically different morphological types. As Douvillé (1913) and many others have shown, the taxodont hinge of the Arcidae represents a late development quite unrelated to the nuculoids.

The Cryptodonta (= Palaeoconcha of authors) are an association of convenience for poorly understood, thin-shelled forms without lateral teeth or a well-developed hinge. Most of the families are limited to the early and middle Paleozoic. *Solemya*, a living protobranch of ancient lineage, is classed as a cryptodont until more can be learned about the Paleozoic forms. It differs morphologically from the nuculoids, and the ctenidia are used in feeding as well as respiration. The cryptodonts were considered by Neumayr, Dall, and Douvillé as primitive burrowers ancestral to many later stocks, but the validity of this idea has been, in part, demonstrated. Most lack the siphonal gape of deep burrowers, and some of the forms included herein may even have been bivalved crustaceans.

The Pteriomorphia (the fixed, or sedentary, branch of Douvillé) are accepted by many paleontologists as a phylogenetic unit. These are the anisomyarians plus the arcoids and Paleozoic cyrtodonts (fig. 3). Although they are morphologically diverse, the fossil record indicates continuity and common origins for several of the lines. It is possible, as Cox (1960) has pointed out, that the Mytilacea had a separate origin in the Modiomorphidae, a group of the Palaeoheterodonta. The duplivincular grade

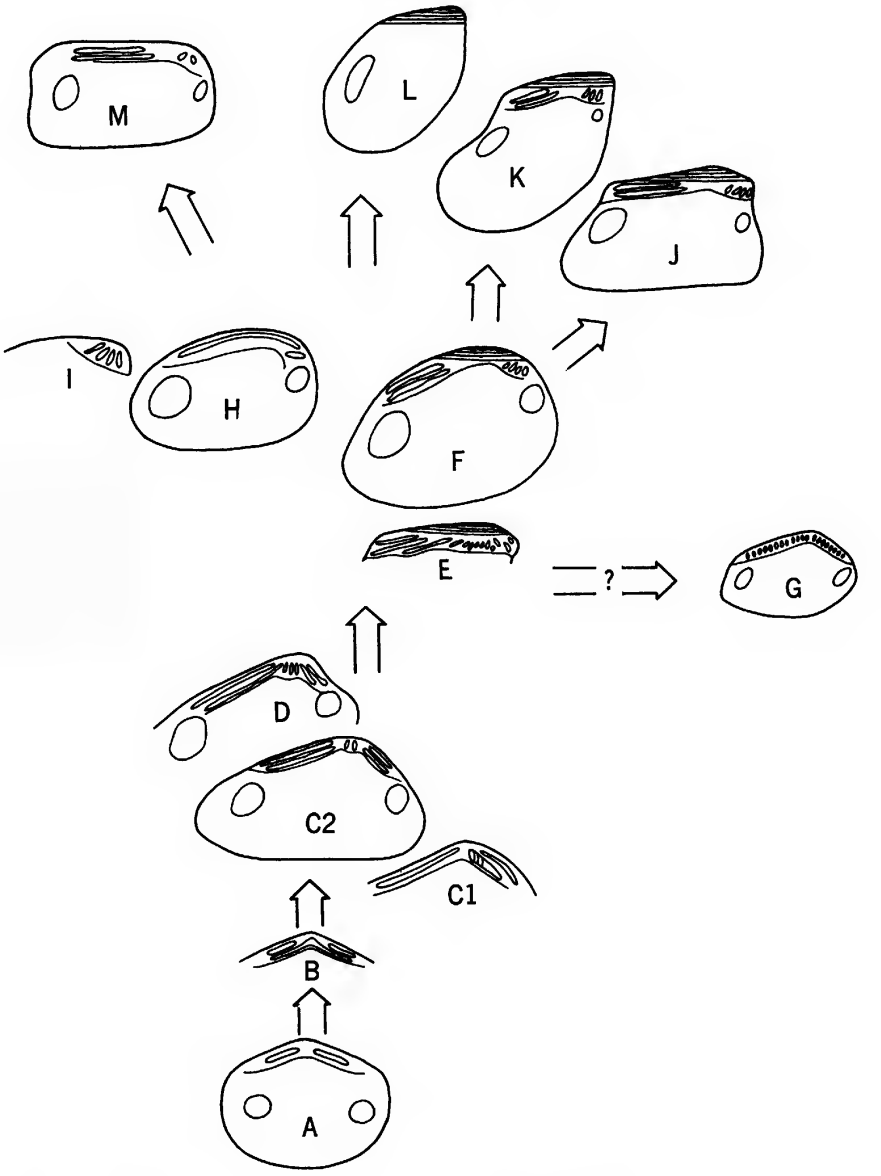

FIG. 3. Radiation of major groups of bivalves in the Paleozoic (modified from Vogel, 1962). A, B. Lamellodontidae, Cambrian. C1, C2, D. Hinge types among the Cycloconchidae, Ordovician. E, F. Cyrtodontidae, Ordovician. G. Nuculoid (*Tancrediopsis*), Ordovician. H, I. Modiomorphidae, Ordovician. J. Parallelodontidae, Ordovician. K. Pterineidae, Devonian. L. Myalinidae, late Paleozoic. N. Permophoridae, late Paleozoic.

of ligament is found in many groups of this subclass, but through parallel trends some of the families have attained the alivincular or parivincular grade of ligament. Characteristically, the Pteriomorphia are members of the epifauna, but a few have adopted a boring habit in firm substrates. Many retain the byssus throughout life, a characteristic of very young bivalves of other groups.

The Palaeoheterodonta comprise the early Paleozoic actinodonts, unionaceans, and trigoniaceans. This grouping may be artificial, but the later members are alike in the possession of free or incompletely fused mantle margins, an opisthodetic parivincular ligament, and prismato-nacreous shells. Posterolateral hinge teeth, where present, originate at the beaks and below the ligament. The actinodonts include the earliest known bivalves (middle Cambrian of Spain; Vogel, 1962). They may have given rise to the Pteriomorphia, the Heterodonta, and possibly other groups.

The Heterodonta differ from the Palaeoheterodonta in possessing non-nacreous shells (complex, or crossed lamellar) and more or less fused, siphonate, mantle margins. Posterolateral teeth, where present, originate some distance behind the beaks and ligament. The ctenidia of living representatives are of the eulamellibranch grade. These animals extend far back into the Paleozoic where they merge gradually with the actinodonts. They nestle or burrow in diverse substrates, and their siphons show appropriate adaptations for depth of penetration beneath the surface.

The Anomalodesmata are generally siphonate, burrowing forms with prismato-nacreous shells, an internal resilium, chondrophores, and a lithodesma. In most groups a hinge plate and teeth are weak or lacking.

THE ORDERS

The long history of work on bivalve classification has been characterized by repeated revisions based on new evidence and new points of view. Usually, new work has resulted in an emendation of the limits of various taxa. Most authors have believed, as did Cox (1960), that extensive emendation renders the old names obsolete. Simpson has commented on this problem: "To demand a change of name whenever such a shift is made would result in utmost confusion and duplication of terminology, and to change the author and date would be unjust and would obscure the historical origin of names and concepts. The opposite view might logically demand recognizing as author the first student to use a name in precisely its present sense. In most cases this would mean either that the technical authors of many time-hallowed names would change constantly and would tend to be the latest revisers, or that revisers were honor-bound not to

change ranks of groups, which would stultify revision" (Simpson, 1945, p. 32).

The problem of obsolescence and repeated replacement of names does not apply to family-group taxa, because they are legally based on type genera. Consequently, anyone may increase or decrease the scope of these taxa without disturbing their nomenclatural stability. They need not retain, even approximately, the limits suggested by the original author, since they are anchored to a nomenclatural type. Obviously, if knowledge is to expand in taxonomy, *a priori* limits cannot be placed on individual taxa. The use of nomenclatural types for orders is a convenient, elastic, and familiar method of insuring stability of nomenclature, while permitting freedom of individual judgment. It obviates any need for rigidly adhering to original definitions or to the endless dropping of names in consequence of emendation. This device has been in steady use for order-group names in many major groups of invertebrates (e.g., brachiopods, cephalopods, coelenterates, echinoids, trilobites, and others), and the practice of anchoring suborders and orders to genera was used for the bivalves by a few nineteenth century taxonomists, as noted above.

References to figure 2 will show that the ordinal groupings adopted here are essentially those of Cox (1960). The changes in names do not require further comment. The number of orders has been reduced from 15 to 14 by the reuniting of the Ostreacea (Colloconchida) with the Pectinacea and related superfamilies on the basis of paleontologic evidence of close relationship (Newell, 1960). Several of the orders contain only one or two superfamilies, but their known history and morphological isolation militate against their being combined at present with other groups. An outline of the subclasses and ordinal group taxa follows. New family-group taxa are omitted from this outline to avoid introduction here of *nomina nuda*.

OUTLINE OF MAJOR DIVISIONS

CLASS BIVALVIA (BONNANI, 1681) LINNAEUS (1758, p. 645)

- SUBCLASS PALAEOTAXODONTA: The nuculoids; nacreous or crossed lamellar; equivalved.
  - ORDER NUCULOIDA: Protobranch taxodonts; Purchon type 1; Stasek type 3; a homogeneous group.
- SUBCLASS CRYPTODONTA: *Solemya* plus Paleozoic cryptodonts; edentulous or nearly edentulous; generally equivalved; probably polyphyletic.
  - ORDER SOLEMYOIDA: *Solemya;* homogeneous aragonite ostracum; siphonate, burrowing protobranchs.
  - ORDER PRAECARDIOIDA, NEW ORDER: Paleozoic cryptodonts; probably a heterogeneous group.

?Order Conocardioida: Paleozoic cryptodonts; anteriorly gaping; cellular shell structure.

Subclass Pteriomorphia: Cyrtodonts, arks, dysodonts; shell structure, ligament, gills, and stomach variable; commonly byssate in adults; phyletic unity suggested by the fossil record.

Order Arcoida: Isomyarian filibranchs with crossed-lamellar shells; cyrtodonts and prionodonts; generally equivalved; Purchon type 3; Stasek type 3.

Order Mytiloida: Anisomyarian, generally equivalved, filibranchs and eulamellibranchs with prismato-nacreous shells; Purchon type 3; Stasek type 1; mainly byssate in adults.

Order Pterioida, New Order: Anisomyarian and monomyarian, mainly pleuroconchs and byssate in adults; filibranchs, eulamellibranchs; nacreous, crossed lamellar, or foliate internally; Purchon types 3 and 4; Stasek type 3.

Subclass Palaeoheterodonta, New Subclass: Early actinodonts, modiomorphaceans, unionaceans, trigoniaceans; prismato-nacreous; Purchon type 4; Stasek type 1.

Order Actinodontoida: Actinodonts; early Paleozoic precursors of most of the orders of bivalves. Teeth absent or radial, poorly differentiated, originating at the beaks; equivalved.

Order Unionoida: Variable upper Paleozoic and post-Paleozoic, nonmarine forms probably derived from the preceding; eulamellibranchs; Purchon type 4; Stasek type 1; probably polyphyletic.

Order Trigonioida: Trigonal marine shells; laterals lacking; filibranchs; homogeneous.

Subclass Heterodonta: Heterodonts; complex crossed-lamellar eulamellibranchs.

Order Hippuritoida, New Order: Pachydonts; mainly attached, extinct forms.

Order Veneroida: Active heterodonts; Purchon types 4 and 5; Stasek types 1, 2, and 3; probably polyphyletic.

Order Myoida: Asthenodonts with degenerate hinge, generally with siphons and united mantle margins; shell complex crossed lamellar; Purchon type 5; Stasek type 3; probably polyphyletic.

Subclass Anomalodesmata: Generally fossorial, without well-developed hinge teeth; generally with siphons, mantle margins united; ligament associated in all but most primitive forms with internal resilium and lithodesma; internally nacreous.

Order Pholadomyoida, New Order: Burrowers with primitive hinge; eulamellibranchs; Purchon type 4; Stasek type 3.

Order Poromyoida: Septibranchs; Purchon type 2; Stasek type 3.

THE HIERARCHY OF TAXONOMIC CATEGORIES

Class Bivalvia Linnaeus, 1758
  Subclass Palaeotaxodonta Korobkov, 1954
    Order Nuculoida Morton, 1963 (as Nuculacea)
      Superfamily Nuculacea Gray, 1824

Family Nuculidae Gray, 1824
Superfamily Nuculanacea Meek, 1864 (Adams and Adams, 1858)
Family Nuculanidae Meek, 1864 (Adams and Adams, 1858)
Family Malletiidae Adams and Adams, 1858
Subclass Cryptodonta Neumayr, 1884
Order Solemyoida Morton, 1963 (as Solemyacea)
Superfamily Solemyacea Adams and Adams, 1857 (Gray, 1840)
Family Solemyidae Adams and Adams, 1857 (Gray, 1840)
Order Praecardioida Newell, new order
Superfamily Praecardiacea Hoernes, 1884
Family Praecardiidae Hoernes, 1884
Superfamily Edmondiacea King, 1850
Family Edmondiidae King, 1850
Family Orthonotidae Miller, 1877
Family Sanguinolitidae Miller, 1877
?Order Conocardioida Neumayr, 1891
Superfamily Conocardiacea Miller, 1889
Family Conocardiidae Miller, 1889
Subclass Pteriomorphia Beurlen, 1944
Order Arcoida Stoliczka, 1871 (as Arcacea)
Superfamily Cyrtodontacea Ulrich, 1893
Family Cyrtodontidae Ulrich, 1893
Superfamily Arcacea Goldfuss, 1820
Family Arcidae Goldfuss, 1820
Family Cucullaeidae Stewart, 1930
Family Noetiidae Stewart, 1930
Family Parallelodontidae Dall, 1898
Superfamily Limopsacea Dall, 1895
Family Limopsidae Dall, 1895
Family Glycymerididae Newton, 1922 (Axinaeinae Adams and Adams, 1858)
?Family Manzanellidae Chronic, 1952
?Family Philobryidae Bernard, 1897
Order Mytiloida Férrusac, 1822 (as Mytillacés)
Superfamily Mytilacea Rafinesque, 1815
Family Mytilidae Rafinesque, 1815
Superfamily Pinnacea Leach, 1819
Family Pinnidae Leach, 1819
Order Pterioida Newell, new order
Suborder Pteriina Newell, new suborder
Superfamily Ambonychiacea Miller, 1877
Family Ambonychiidae Miller, 1877
Family Myalinidae Frech, 1891
Family Lunulacardiidae Fischer, 1887
Superfamily Pteriacea Gray, 1847
Family Pteriidae Gray, 1847
Family Bakevelliidae King, 1850
Family Cassianellidae Ichikawa, 1958
Family Dattidae Healey, 1908

Family Inoceramidae Giebel, 1852
Family Isognomonidae Woodring, 1925
Family Kochiidae Maillieux, 1931
Family Malleidae Gray, 1823
Family Pterineidae Miller, 1877
Family Pulvinitidae Stephenson, 1941
Superfamily Pectinacea Rafinesque, 1815
Family Pectinidae Rafinesque, 1815
Family Aviculopectinidae Meek and Hayden, 1864
Family Buchiidae Cox, 1953
Family Deltopectinidae Dickens, 1957
?Family Dimyidae P. Fischer, 1886
Family Monotidae Fischer, 1886
Family Oxytomidae Ichikawa, 1958
Family Entoliidae Korobkov, 1960
Family Plicatulidae Watson, 1930
Family Posidoniidae Frech, 1909
Family Pseudomonotidae Newell, 1938
Family Pterinopectinidae Newell, 1938
Family Spondylidae Gray, 1826
Superfamily Anomiacea Rafinesque, 1815
Family Anomiidae Rafinesque, 1815
Superfamily Limacea Rafinesque, 1815
Family Limidae Rafinesque, 1815
Suborder Ostreina Férrusac, 1822 (as Ostracés)
Superfamily Ostreacea Rafinesque, 1815
Family Ostreidae Rafinesque, 1815
Subclass Palaeoheterodonta Newell, new subclass
Order Actinodontoida Douvillé, 1912 (as Actinodonta)
Superfamily Modiomorphacea Miller, 1877
Family Modiomorphidae Miller, 1877
Family Cycloconchidae Ulrich, 1893 (Allodesmidae Dall, 1895)
Family Lamellodontidae Vogel, 1962
Family Carydiidae Haffner, 1959
Order Unionoida Stoliczka, 1871 (as Unionacea)
Superfamily Anthracosiacea Amalitzky, 1892
Family Anthracosiidae Amalitzky, 1892
Family Ferganoconchidae Martinson, 1956
Family Pseudocardiniidae Martinson, 1961
Superfamily Unionacea Fleming, 1828
Family Unionidae Fleming, 1828
Family Desertellidae Dechaseaux, 1946
Family Etheriidae Swainson, 1840
Family Margaritiferidae Ortmann, 1912
Family Mutelidae Gray, 1847
?Family Pachycardiidae Cox, 1961
Order Trigonioida Dall, 1889 (as Trigoniacea)
Superfamily Trigoniacea Lamarck, 1819
Family Trigoniidae Lamarck, 1819

?Family Lyrodesmatidae Ulrich, 1894
Family Myophoriidae Cox, 1952
?Family Scaphellinidae Newell and Ciriacks, 1962
?Family Trigonioididae Cox, 1952
Subclass Heterodonta Neumayr, 1884
Order Hippuritoida Newell, new order
Superfamily Chamacea Gray, 1823
Family Chamidae Gray, 1823
Superfamily Megalodontacea Morris and Lycett, 1853
Family Megalodontidae Morris and Lycett, 1853
Superfamily Hippuritacea Gray, 1848
Family Hippuritidae Gray, 1848
Family Caprinidae Meek, 1864
Family Caprotinidae Gray, 1848
Family Diceratidae Dall, 1895
Family Monopleuridae Munier-Chalmas, 1873
Family Radiolitidae Gray, 1848
Family Requieniidae Douvillé, 1914
Order Veneroida Adams and Adams, 1858 (as Veneracea)
Suborder Lucinina Dall, 1889 (as Lucinacea)
Superfamily Lucinacea Fleming, 1828
Family Lucinidae Fleming, 1828
Family Babinkidae Horný, 1960
Family Cyrenoididae Adams and Adams, 1857
Family Fimbriidae Nicol, 1950 (Dall, 1895)
Family Mactromyidae Cox, 1929 (Fischer, 1887)
Family Thyasiridae Dall, 1901
Family Ungulinidae Adams and Adams, 1857
Superfamily Leptonacea Gray, 1847 (Erycinacea Deshayes, 1850)
Family Leptonidae Gray, 1847
Family Chlamydoconchidae Dall, 1900
Family Erycinidae Deshayes, 1850
Family Gaimardiidae Hedley, 1916
Family Galeommatidae Gray, 1847
Family Kelliidae Clark, 1851
Family Montacutidae Clark, 1855
Superfamily Cyamiacea Sars, 1878
Family Cyamiidae Sars, 1878
Family Neoleptonidae Thiele, 1934
Family Turtoniidae Clark, 1855 (Sportellidae Dall, 1900)
Superfamily Carditacea Fleming, 1828
Family Carditidae Fleming, 1828
Family Condylocardiidae Bernard, 1897
Family Permophoridae Van der Poel, 1959 (Dall, 1895)
Superfamily Crassatellacea Menke, 1830
Family Crassatellidae Menke, 1830
Family Astartidae d'Orbigny, 1844
Family Cardiniidae Zittel, 1881
Superfamily Cardiacea Goldfuss, 1820

Family Cardiidae Goldfuss, 1820
Family Adacnidae Von Vest, 1875
Family Lahilliidae Marwick, 1944
Superfamily Tridacnacea Goldfuss, 1820
Family Tridacnidae Goldfuss, 1820
Superfamily Mactracea Gray, 1823
Family Mactridae Gray, 1823
Family Anatinellidae Gray, 1853
Family Cardiliidae Fischer, 1887
Family Mesodesmatidae Gray, 1840
Superfamily Solenacea Gray, 1823
Family Solenidae Gray, 1823
Family Cultellidae Davies, 1935
Superfamily Tellinacea Latreille, 1825
Family Tellinidae Latreille, 1825
Family Donacidae Fleming, 1828
Family Garidae Stoliczka, 1871 (Fleming, 1828)
Family Icanotiidae Casey, 1961
Family Quenstedtiidae Cox, 1929
Family Scrobiculariidae Adams and Adams, 1856
Family Semelidae Stoliczka, 1870
Family Solecurtidae d'Orbigny, 1846
Family Sowerbyidae Cox, 1929
Family Tancrediidae Meek, 1864
Suborder Arcticina Newell, new suborder
Superfamily Arcticacea Newton, 1891 (Woodward, 1854)
Family Arcticidae Newton, 1891 (Woodward, 1854)
Family Euloxidae Gardner, 1943
Family Trapeziidae Lamy, 1920
Superfamily Dreissenacea Gray, 1840
Family Dreissenidae Gray, 1840
Superfamily Glossacea Gray, 1847 (Isocardiacea Gray, 1840)
Family Glossidae Gray, 1847 (Isocardiidae Gray, 1840)
Family Dicerocardiidae Kutassy, 1934
Family Kelliellidae Fischer, 1887
Family Vesicomyidae Dall, 1908
Superfamily Corbiculacea Gray, 1847
Family Corbiculidae Gray, 1847 (Gray, 1840)
Family Pisidiidae Gray, 1857
Superfamily Veneracea Rafinesque, 1815
Family Veneridae Rafinesque, 1815
Family Cooperellidae Dall, 1900
Family Glauconomidae Gray, 1853
Family Petrocolidae d'Orbigny, 1839
Family Rzehakiidae Korobkov, 1954
Order Myoida Stoliczka, 1870 (as Myacea)
Suborder Myina Newell, new suborder
Superfamily Myacea Goldfuss, 1820
Family Myidae Goldfuss, 1820

Family Corbulidae Gray, 1823
Family Erodontidae Winckworth, 1932
Family Megadesmatidae Fischer, 1887
Family Pleurodesmatidae Cossmann and Peyrot, 1909
Family Raetomyidae Newton, 1919
Family Spheniopsidae Gardner, 1928
Superfamily Gastrochaenacea Gray, 1840
Family Gastrochaenidae Gray, 1840
Superfamily Hiatellacea Gray, 1824
Suborder Pholadina Newell, new suborder
Superfamily Pholadacea Rafinesque, 1815
Family Pholadidae Rafinesque, 1815
Family Teredinidae Latreille, 1825
Subclass Anomalodesmata Dall, 1889
Order Pholadomyoida Newell, new order
Suborder Pholadomyina Newell, new suborder
Superfamily Pholadomyacea Fleming, 1828
Family Pholadomyidae Gray, 1847
Family Burmesiidae Healey, 1908
Family Ceratomyidae Arkell, 1934
Family Pleuromyidae Dall, 1900
Superfamily Pandoracea Rafinesque, 1815
Family Pandoridae Rafinesque, 1815
Family Cleidothaeridae Hedley, 1918 (Fischer, 1887)
Family Laternulidae Hedley, 1918 (Anatinidae Gray, 1840)
Family Lyonsiidae Fischer, 1887
Family Myochamidae Bronn, 1862
Family Periplomatidae Dall, 1895
Family Thraciidae Stoliczka, 1871
Suborder Clavagellina Newell, new suborder
Superfamily Clavagellacea d'Orbigny, 1845
Family Clavagellidae d'Orbigny, 1845
Order Poromyoida Pelseneer, 1906 (as Poromyacea)
Superfamily Poromyacea Dall, 1886
Family Poromyidae Dall, 1886
Family Cuspidariidae Dall, 1886
Family Verticordiidae Stoliczka, 1870

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